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*Published in:*  
Ecotropica

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*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2007

[Link to publication in University of Groningen/UMCG research database](#)

### *Citation for published version (APA):*

Freymann, B. P., Visser, S. N. D., Mayemba, E. P., & Olff, H. (2007). Termites of the Genus *Odontotermes* are Optionally Keratophagous. *Ecotropica*, 13(2), 143-147.

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## TERMITES OF THE GENUS *ODONTOTERMES* ARE OPTIONALLY KERATOPHAGOUS

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**Abstract.** In this study we tested experimentally whether the consumption of mammalian hooves by termites of the genus *Odontotermes* is a mere incidental, previously overlooked event, or whether higher termites frequently exploit hooves of ungulates as a supplementary food source. The experiment was conducted in the open woodland savanna region of Serengeti National Park, Tanzania. In total, 88 hooves of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) – of two age classes – were offered to the termites in the field. After five days, 18.3% of old and 15.0% of fresh wildebeest hooves and 16.7% of old zebra hooves were utilized by termites as a food source. Accordingly, we report here for the first time a systematic, frequent necrophorous foraging behavior of termites in general, which also adds termites to the very short list of potential decomposers of mammalian hooves. Termites of the genus *Odontotermes* seem not to show a preference for a specific age class of the provided wildebeest hooves. Our results suggest that ungulate hooves represent a spatially and temporally highly variable, potentially macro- and micronutrient-rich, supplementary food source for higher termites in this savanna ecosystem. Termites of the genus *Odontotermes* might accordingly be considered as being not only decomposers, but also optional necrophores, i.e. being keratophagous. Members of this genus might play an important role in the decomposition of mammalian hooves in African savannas. Accepted 6 August 2007.

**Key words:** Hooves, invertebrate necrophores, nutritional demands, *Odontotermes*, savanna, Serengeti National Park, Tanzania, wildebeest carcasses.

### INTRODUCTION

Termites are distributed throughout the tropical and subtropical regions of the world, with the highest species diversity found in tropical forests (Eggleton 2000). For the Afrotropics approximately 660 species belonging to about 170 genera are currently described (Uys 2002). Termites are known as either herbivores or decomposers, feeding on a whole range of living, recently dead, or dead plant material in various stages of decomposition (Wood 1978). Also soil rich in organic matter and fungi are consumed frequently.

In addition to these food items, Wood (1978) lists “skins, etc. of vertebrate corpses” without further specification as “special or incidental foods” of termites. A thorough examination of the existing literature revealed that only a very few anecdotal publications exist on necrophorous feeding habits of termites. Records reporting that termites do feed on vertebrate carcasses in various stages of decay can be placed into two groups: Derry (1911), Watson and Abbey (1986), and

Kaiser (2000) document or speculate on the possibility of termites preying on fossilized or several-years-old skulls and bones in Africa (Derry 1911, Kaiser 2000) and Australia (Watson & Abbey 1986). In contrast to these records, Thorne and Kimsey (1983) report termites of the genus *Nasutitermes* utilizing a complete fresh mammalian carcass as a food source. This record stems from the Neotropics. In India, termites of the genus *Odontotermes* have been observed to feed on tusks in museum collections (Eggleton pers. comm.). Also, the existing literature on the dynamics of carrion arthropod assemblages (e.g., Braack 1987, Schoenly & Reid 1987) does not attribute to termites more than an incidental role in the decomposition of vertebrate carcasses, citing only one single record where termites were observed on carcasses (Early 1985).

In July 2005 we made an accidental finding in the mixed grass region of Serengeti National Park (SNP), Tanzania: we found the remnants of a Grant's gazelle (*Gazella granti*) carcass, whose hooves were covered by so called “sheeting”. Sheeting consists of a mixture of soil particles, termite saliva, and termite feces and

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is used by these Isoptera to construct foraging tunnels in order to protect them from harmful direct exposure to sunlight. The covering of a given material with sheeting indicates that termites have used the same material as a food source. Accordingly, this finding represents the first record of termites utilizing mammalian hooves as a food source and stimulated this experimental field study.

SNP is located in the north of Tanzania as part of the wider Serengeti-Mara ecosystem (1°15'–3°30'S, 34°–36°E). Sized about 25 000 km<sup>2</sup> it is home to the largest herd of migrating ungulates in the world, with about 1.2 million wildebeests (*Connochaetes taurinus*), as well as about 200 000 zebras (*Equus burchelli*) and more than 400 000 Thomson's gazelles (*Gazella thomsoni*) (Sinclair 1995, Packer *et al.* 2005). These mammalian herbivores are heavily preyed upon by a number of predators, among them spotted hyenas (*Crocuta crocuta*), which consume virtually all parts of their prey besides the rumen contents, horns, and hooves (Cooper *et al.* 1999).

The aim of this study was to test experimentally whether the consumption of the Grant's gazelle hooves by termites was a mere incidental observation or whether the termites inhabiting the Serengeti-Mara ecosystem frequently exploit hooves as a supplementary food source, showing potentially a preference for wildebeest or zebra hooves. If so, the utilization of mammalian hooves as a food source would not only represent an interesting amendment to the existing food list of termites but also broaden our understanding of the functional role of termites in this ecosystem. To our knowledge, this study is the first field experiment conducted on the use of this food source by termites.

## METHODS

**Study site.** This study was conducted in November 2005 in the vicinity of the Seronera Research Centre, Serengeti National Park, Tanzania (2°26'S, 34°51'E, 1535 m a.s.l.). The prevailing habitat type at the study site is an open woodland savanna.

**Field experiment.** In the wider surroundings of the Research Centre a total of 60 old and 22 fresh hooves of blue wildebeest (*Connochaetes taurinus*) and 6 old hooves of Burchell's zebra (*Equus burchelli*) were collected by dissecting them from carcasses that were found randomly alongside roads during a search over several days. "Old" hooves were defined as originating from skeletons, whereas "fresh" hooves stemmed

from carcasses that still contained remnants of dermal and muscular tissue. At the study site 10 termite mounds were chosen that appeared to be actively inhabited by termites, as indicated by signs of recent construction or foraging behavior. The chosen mounds were spaced at about 50–250 m from each other, a distance that should be sufficient to ensure that the mounds were of separate colonies. This distance was chosen based on published information on foraging distances of termites: Banerjee (1975) found a foraging area of 4 m<sup>2</sup> for a 70-cm-high mound of *Odontotermes redemanni* in India; Darlington (1982) reported that the main foraging zone of *Macrotermes michaelseni* is 10–35 m from the nest, while Coaton (1958) mentioned that *Microhodotermes viator* forages in a radius of approximately 45 m from the hive site. At the base of each mound, six old wildebeest hooves were placed randomly in such a way that they were in direct contact with the soil. Additionally, at the base of eight mounds two fresh wildebeest hooves, at the base of two mounds three fresh wildebeest hooves, as well as at the base of six mounds one zebra hoof each were placed in the same way. Hooves were placed in the field on 29 October and checked 5 days later for signs of termite activity: either direct sightings of termites or the presence of sheeting. Previous field experiments revealed that 5 days is a sufficient time span in which termites are able to detect and use a new food source (Freyman & De Visser unpubl. data). Hooves were placed only at spots without signs of old sheeting. In the case of a direct encounter with termites while checking the hooves, termite soldiers were collected for later identification in the laboratory.

**Laboratory analysis.** Termite specimens were identified to genus level at the University of Groningen, The Netherlands, using a microscope and the key by Uys (2002).

## RESULTS

The percentages of hooves fed on by termites in the conducted field experiment are given in Table 1. Five days after initial placement in the experimental plots, 18.3% of all old wildebeest hooves, 15.0% of all fresh wildebeest hooves, and 16.7% of all old zebra hooves were exploited by termites as a food source. Utilization was indicated either directly through sightings of individual termites at the hooves and the detection of foraging marks on the hooves – the blackish outer surfaces which were in contact with the soil were sealed off by termite sheeting, scraped off, and the

TABLE 1. Percentages of wildebeest (WB) and zebra (Z) hooves (this experiment), as well as WB dung and grass litter baits (unpubl. data Freymann & De Visser), fed on by termites of the genus *Odontotermes* during the wet season in Serengeti National Park, Tanzania.

Food source	% utilized after 5 days	Sample size (# replicates)
Old WB hooves	18.3	N = 6 (10)
Fresh WB hooves	15.0	N = 2 (10)
Old Z hooves	16.7	N = 1 (6)
Fresh WB dung	4.2	N = 6 (20)
Dry grass litter	1.7	N = 6 (20)

inner whitish layers were clearly visible. Or the utilization of these hooves was indicated indirectly by the occurrence of termite sheeting. Also 25 days after placement in the field, fresh signs of utilization by termites were still encountered at the baits, but due to methodological constraints these observations were not comparable to the frequencies given above.

The collected specimens were identified as soldiers of the genus *Odontotermes*, but could not be identified to species level.

## DISCUSSION

Firstly, this study documents that termites of the genus *Odontotermes* indeed use ungulate hooves systematically as a food source. Given the consumption frequencies as listed in Table 1, the utilization of this food source has to be regarded as of more than extremely rare, incidental importance. This is also supported by the finding that termites fed in this experiment on both wildebeest and zebra hooves in addition to the initial observation of feeding on Grant's gazelle hooves. Furthermore, the exploitation frequencies of hooves as a food source have to be judged as more than incidental when seen in comparison to the following background data (Freymann & De Visser unpubl. data). In a separate experiment we quantified the utilization of fresh wildebeest dung and dry grass litter by *Odontotermes* within the same time span and the same season in SNP. As given in Table 1, 4.2% of the provided fresh wildebeest dung baits and 1.7% of the dry grass litter baits were fed on by termites in the first 5 days after placement in the field. Mammalian dung and dry grass litter are common

food sources of *Odontotermes* (Freymann pers. obs.). The actual consumption rates of these two resources might be slightly higher than shown by this separate experiment if these resources had been placed as close to the mounds as in this study and in the absence of all other grass litter sources besides the studied samples, which was not the case. In this separate experiment, dung and litter baits were placed approximately 25 m away from mounds. Nevertheless, it appears justified to state that our field experiment shows that the *Odontotermes* termites inhabiting the Serengeti-Mara ecosystem do frequently exploit mammalian hooves as a supplementary food source. Due to our too small sample sizes we are not able to test statistically whether these termites show a preference for wildebeest or zebra hooves or for one age class of wildebeest hooves, but visual inspection of the data suggests that this is not the case.

Termites of the genus *Odontotermes* are fungal growers, normally consuming a wide variety of plant material ranging from wood to grass (Freymann & De Visser unpubl. stable isotope data), as well as crops including eucalyptus, pine, wattle tree, cotton and maize (Uys 2002). Our field study is, to our knowledge, the first one worldwide to experimentally document the use of mammalian hooves as a food source for termites in general. As summarized earlier, there are a few anecdotal publications on necrophorous feeding habits of termites. Any record of such a foraging behavior shown by termites is remarkable in that termites are regarded predominantly as decomposers, exclusively of plant materials, and not of animal tissues. Accordingly, the novelty of our findings is twofold: it represents the first ever record of termites feeding on hooves, an animal tissue, and perhaps of greater importance, we report here for the first time the systematic, frequent occurrence of a necrophorous (keratophagous) foraging behavior in termites, in contrast to the merely coincidental, anecdotal reports published earlier of termites feeding on bones and skulls (Derry 1911, Kaiser 2000). In addition, our observations are interesting because they add such a diverse and abundant invertebrate group as termites to the very short list of potential decomposers of mammalian hooves, including (e.g.) carrion beetles and moth-grubs of the genus *Ceratophaga* (Tineidae, Lepidoptera). Termites of the genus *Odontotermes* might in this way contribute to the re-entry of the nutrients contained in mammalian hooves into the nutrient cycle. Moreover, our findings may have further ecological implications.

Termites usually have to get by on a nitrogen poor diet (e.g., Ohkuma *et al.* 2001). Among the lower termites – a group of six evolutionarily distinct termite families – nitrogen fixation by microorganisms inhabiting the gut is a commonly observed phenomenon (Ohkuma *et al.* 2001). The genus *Odontotermes*, though, belongs to the Macrotermitinae in the family Termitidae, the higher termites, and Ohkuma and coworkers (2001) could not detect any nitrogen fixation activity in the examined species *Odontotermes formosanus*. The higher termites in general display only low nitrogen fixation activity, but show instead variation in their diet as well as extensive foraging behavior, probably in order to acquire nitrogen from their food (Ohkuma *et al.* 2001). Fungus-growing termites in particular, such as *Odontotermes*, are considered to be not nitrogen limited as they use the fungus to burn off carbon and so improve the C/N ratio of their food. Still the hoof-feeding habit documented here might be for termites one additional behavioral strategy to survive in a nitrogen-limited ecosystem. Prior to the conducted experiment (mid July 2005) a human-induced fire removed most of the dead plant biomass from the study site. After the onset of a very short rainy season in September 2005, plant regrowth was observed at the study site, attracting a high abundance and diversity of mammalian herbivores to the locality. This in turn led to an extensive grazing phase leaving only very little plant biomass behind at the time this experiment was set up. We observed that the termites mainly fed on the sole of the hooves provided, which consists of horn. However, as a protein, horn is rich in nitrogen (Stryer 1996). Therefore we take the view that one possible explanation for the observed behavior might be that termites of the genus *Odontotermes* exploit this food source as a supplementary source of nitrogen. Another potential explanation might be that termites feed on mammalian hooves in order to fulfill their need for certain micronutrients. Termites host a wide variety of microbes in their gut, which in turn require certain micronutrients for their physiological processes. A thorough search of the literature did not yield any data on the micronutrient contents of wildebeest and zebra hooves. Without these data and further field experiments it has to remain speculative which role micronutrients play in this context. In times of a shortage of their usual plant diet and during an increased availability of mammalian carcasses (during the annual wildebeest and zebra migration) this feed-

ing behavior might be adaptive in order to fulfill the termites' macro – and micro-nutritional demands. Therefore termites of the genus *Odontotermes* might be considered as being predominantly herbivores and decomposers, but also optional necrophores.

Hooves therefore represent a spatially and temporally highly variable, supplementary food source for some higher termites in this savanna ecosystem. In order to answer the question of how essential this food source is for *Odontotermes* termites, clearly further studies are needed. A potential, positive correlation between the geographical distribution of hoofed mammals and *Odontotermes* termites, as well as the potential finding that *Odontotermes* colonies suffer in some way if hoofed mammals are spatially excluded from their foraging grounds, would prove a hypothetical importance of this food source. In order to assess the overall importance of our findings, it is also desirable to repeat this experiment during different seasons. Our study suggests that higher termites of the genus *Odontotermes* might play an important role in the decomposition of mammalian hooves in African savanna ecosystems.

## ACKNOWLEDGMENTS

We thank the Tanzanian Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA), and the Tanzanian Commission of Science and Technology (COSTECH) for their permission to work in the Serengeti. We would like to thank P. Eggleton and two anonymous referees for critical comments on the manuscript, R. Hoare for insightful discussion, H.A.J. Meijer (CIO) for help with an exploratory stable isotope diet study, and Y. Byarugaba for help in the field. B.P.F. and H.O. were financially supported by the Robert Bosch Foundation (Germany) and the Netherlands Organization for Scientific Research.

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